AUTECOLOGY AND DISTRIBUTION OF THE SILURIAN BRACHIOPOD *DUBARIA*

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ABSTRACT. Smooth-shelled atrypoid brachiopods, *Dubaria varians* (Poulsen, 1943) and *Dubaria* sp. nov., occur in Llandovery strata of western North Greenland in cryptic habitats associated with biostromes and reefs. This ecological preference probably explains their patchy spatial and temporal distribution. It may explain the stratigraphic distribution of *Dubaria* since other species in the genus also occur in association with reefs. External morphological features of *Dubaria* are comparable with the morphological adaptions of a species of *Atrypoidea* which lived in direct association with reefs in the upper Silurian of Arctic Canada.

AUTECOLOGY can be important to biostratigraphy since the interactions between single species and their environments may ultimately control their stratigraphic distribution. Inherent to the topic is the establishment of the environment in which the species lived, for without that knowledge it is impossible to examine the autecology of the species concerned. In some instances the nature of the environment has been inferred from the fossils themselves, a practice that ultimately leads to circular arguments once the autecology of the species is considered. The Silurian–Devonian brachiopod *Dubaria* provides an excellent example of how the knowledge of autecology assists in the understanding of the stratigraphic distribution of a genus or a species.

Boucot and Perry (1981, p. 212) argued that the low diversity *Dubaria* Community inhabited a quiet-water environment since the brachiopod shells are virtually always articulated and show no sign of abrasion. Thus, it might be expected that *Dubaria* would be a common element of Silurian–Devonian faunas for there is ample evidence that quiet-water environments were common in that time period. This is especially true in the light of the comment by Johnson *et al.* (1978, p. 803) that '. . . *Dubaria* is more of a biofacies indicator than a biochronological tool . . .'. However, as demonstrated in this paper, *Dubaria* evidently had particular ecological needs that served to restrict its occurrence to a well-defined ecological niche.

This paper utilizes occurrences of *Dubaria* on a world-wide basis (Table 1) and from western North Greenland (Table 2) to outline the ecological factors that controlled the distribution of the genus.

DUBARIA IN NORTH GREENLAND

Spatial and temporal distribution

Dubaria were found at ten localities in North Greenland (text-fig. 1 and Table 2). Although strata between these localities were examined in detail, no further specimens of *Dubaria* were found. The stratigraphic distribution of *Dubaria* is similarly patchy; although it has been recorded at five different horizons in the Llandovery of North Greenland, strata between those horizons apparently contain no specimens of the genus (text-fig. 2 and Table 2).

This patchy spatial and temporal distribution suggests that other factors such as ecological requirements probably controlled the distribution of *Dubaria*.

Ecological distribution

At Kap Schuchert, *D. varians* and *Dubaria* sp. nov. occur in the uppermost part of the Alegatsiaq Fjord Formation in direct association with small, localized biostromes that are surrounded by

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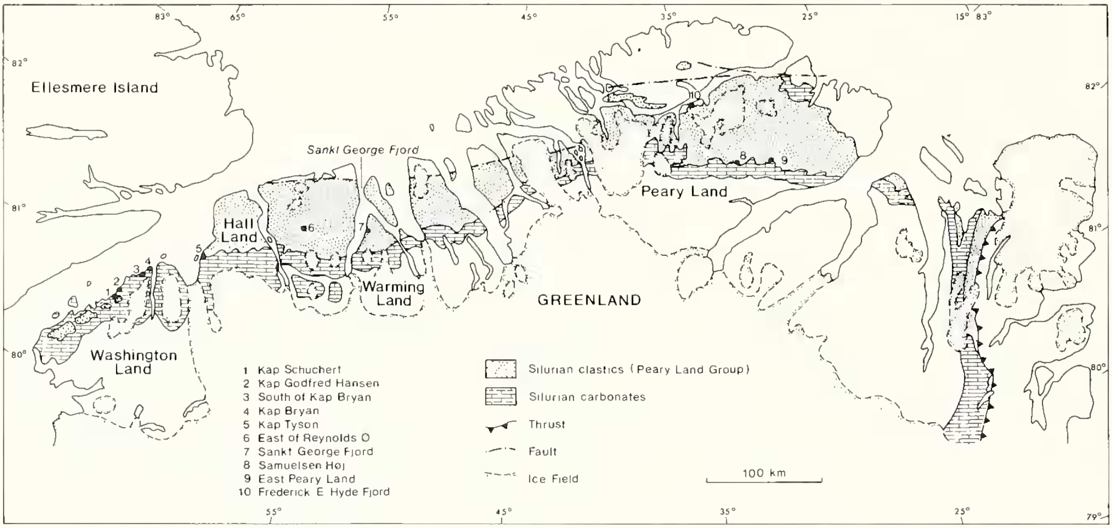
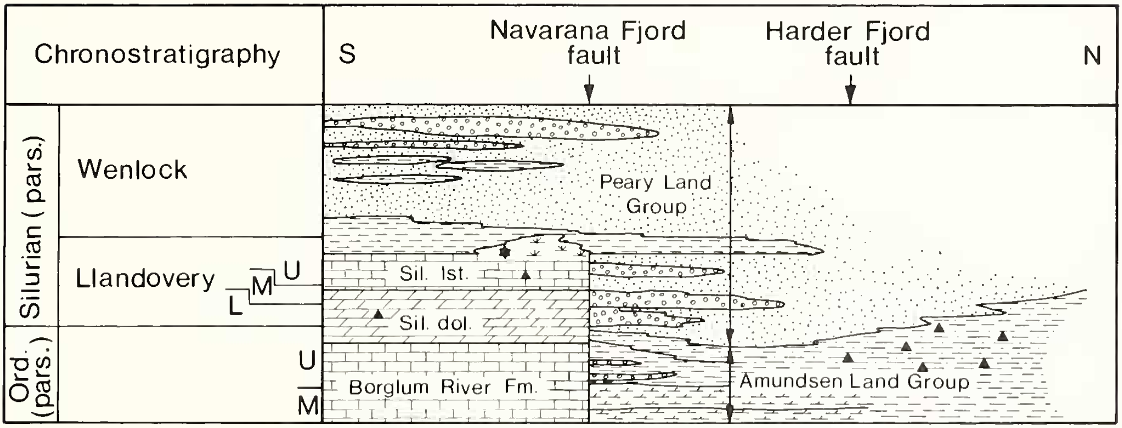
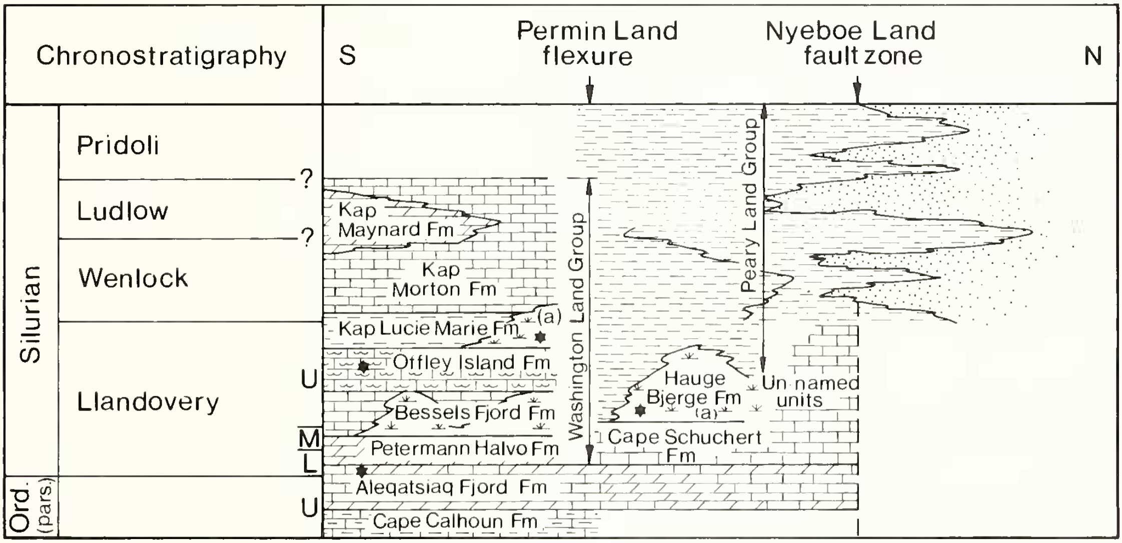


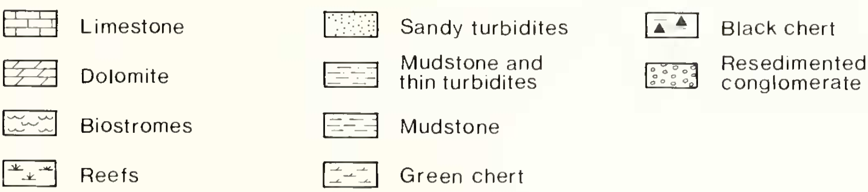
TEXT-FIG. 1. Distribution of Silurian platform carbonates (Hurst 1980) and deep-water basin clastic sediments (Hurst and Surlyk 1982) on North Greenland. Localities 1 to 10 indicate where *Dubaria* were collected (Table 1).

TABLE 1. Recorded occurrences of *Dubaria*. Note the patchy spatial and temporal ranges of the genus as well as the species. * indicates species for which material has been studied.

Species	Reference	Geographic location	Stratigraphic level
D. varians	This paper	NW Greenland	Llandovery*
D. reclinis	Rubel 1970	Estonia	Llandovery*
D. sp. nov.	This paper	NW Greenland	Llandovery*
D. legrinus	Ivanovskii and Kulkov 1974	Altai-Sajan	Upper Llandovery
D. tenera	Nikiforova and Modzalevskaya 1968	Siberia	Llandovery
D. rongxiensis	Wan 1978	Tsuei-shan Yung Tzi Province, China	Middle Silurian
D. sp. D	Johnson *et al.* 1976	Central Nevada	Lower-middle Ludlow
D. sp.	Johnson *et al.* 1976	Central Nevada	Lower-middle Ludlow
D. lentenoisi	Termier 1936	North Africa	Lower Ludlow*
D. megaeroides	Johnson *et al.* 1973 Johnson and Boucot 1970	Central Nevada	Upper Pridoli
D. sp.	Johnson, 1973	Central Nevada	Middle Lochkovian
D. thesis	Johnson, 1975 Smith 1980	Arctic Canada	Upper Lochkovian
D. sp.	Johnson and Boucot 1970	Carnic Alps	Budnanian (Ludlow and Pridoli)







TEXT-FIG. 2. (*Above*) Stratigraphic scheme for Peary Land, North Greenland (from Surlyk *et al.* 1980 and Surlyk and Hurst 1984). (*Below*) Stratigraphic scheme for western North Greenland based on Washington Land and Hall Land (Surlyk and Hurst 1984). Asterisks indicate stratigraphic location of *Dubaria* (Table 2).

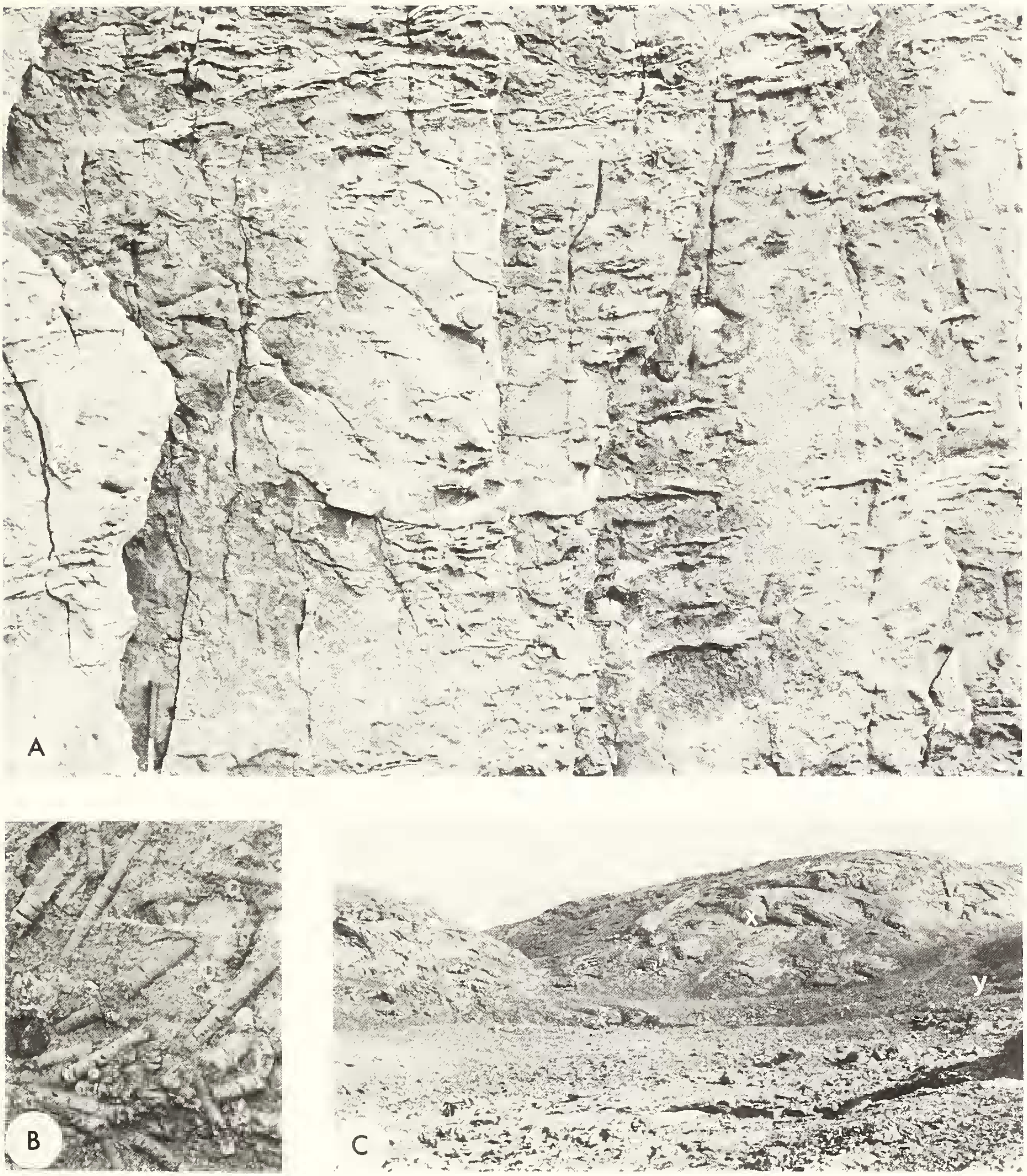
crinoidal rudstones (text-fig. 3). The poorly sorted nature of these rocks and the abundant coral and stromatoporoid colonies, many of which are overturned, suggests accumulation in relatively high-energy, shallow-water carbonate shelf environments. The isolated pockets of skeletal sands, which occur as isolated pockets up to 10 m thick and several tens of metres long, may represent the remains of skeletal sand shoals (Hurst 1980).

The Offley Island Formation represents a carbonate shelf, biostromal unit consisting of level-bedded stromatoporoid floatstones and skeletal, crinoidal, and stromatoporoid rudstones (text-fig. 3) associated with small reefs (Hurst 1980). The biostromes probably represent skeletal sand shoals that accumulated in an agitated, shallow-water subtidal carbonate platform environment. An undulatory sea-floor topography is reflected by the complex vertical and lateral relationship of the facies. The rare laminated pellet lime mudstones probably accumulated in the lower energy environments. that existed in the topographic lows between the sand shoals. *Dubaria* occurs only in the higher energy skeletal sand shoals, never in the low-energy pelletal lime mudstones. Large *D. varians* from upper Llandovery reefs (text-fig. 3c) also occur in pockets and as skeletal components in debris beds, suggesting that they inhabited high energy environments.

Dubaria occurrences in North Greenland are associated with high-energy biostromes and/or reef environments. Contrary to this opinion, Boucot and Perry (1981, p. 212) argued that the low diversity *Dubaria* Community inhabited a quiet-water environment. This dichotomy may reflect the scale at which environmental factors are viewed. Clearly, on a large scale the environment is a high energy one. However, even modern day, high-energy reefal environments encompass quiet, cryptic habitats that on a local scale are quite different in character. For example, Logan (1977) demonstrated that the modern brachiopods *Thecidellina barretti*, *Argyrotheca* sp., and *Platidia* sp. inhabit deep recesses in Eden's Rock, a large patch reef off the coast of Grand Cayman Island. Such recesses typically have little light and little water movement (Logan 1977, p. 91). Logan argued that intense predation pressures and severe competition for space forced the brachiopods to inhabit such cryptic habitats. The analogy with *Dubaria* is striking.

TABLE 2. Summary information on *Dubaria* from west North Greenland. * Geological Survey of Canada locality number. *Dv* = *Dubaria varians*; *D* = *Dubaria* sp. nov.

Locality	Species	Locality on Text-fig. 1	Collector	Formation	Age	Number of Specimens
256354	*Dv*	10	Mabillard	Unnamed Carbonate Reefs	Llandovery to early Wenlock	10
256357	*Dv*	10	Mabillard			57
82370	*Dv*	7	Dawes	Unnamed Carbonate Reefs	?	2
82368	*Dv*	7	Dawes		?	4
82367	*Dv*	7	Dawes		?	5
184128	*Dv*	9	Peel	Unnamed Carbonate Reefs	Llandovery to early Wenlock	1
211789	*Dv*	2	Norford	Aleqatsiaq Fjord Fm.	early Llandovery	2
211765	*D*	6	Norford	Offley Is. Fm.	Llandovery to early Wenlock	4
216887	*D*	2	Hurst	Aleqatsiaq Fjord Fm.	early Llandovery	1



TEXT-FIG. 3. A, biostrome of laminar stromatoporoids and bioclastic debris, Offley Island Formation, Hall Land. B, crinoidal rudstone, Offley Island Formation, Hall Land. C, carbonate buildup (x) surrounded by off-reefal sediments (y) in Peary Land. *Dubaria varians* occurs in both reefs and biostromes. See text-figs. 1 and 2 for location and stratigraphy.

WORLDWIDE DISTRIBUTION OF *DUBARIA*

Dubaria occurs at many different, widely separated localities throughout the world (Table 1). As on Greenland, the stratigraphic distribution of *Dubaria* on a world-wide basis is also patchy (Table 1). For example, *Dubaria* is found in Llandovery strata but only rarely in the Wenlock (Table 1). These patchy spatial and temporal distributions also suggest that ecological factors may have controlled the occurrences of this brachiopod on a wide scale. Unfortunately, this suggestion cannot always be verified because the sedimentological setting of *Dubaria* is commonly not documented.

Atrypopsis reclinis Rubel (= *D. reclinis*) is common in the Llandovery strata on the Estonian island of Hiiuma in the northern Baltic. Rubel (1983 written comm.) states that 'the known distribution of *Atrypopsis reclinis* in the North Baltic is really restricted to the bioherms or related rocks'. *D. lantenoisi*, the type species of the genus, occurs in the Ludlow of Morocco (Termier 1936). Termier and Termier (1960, fig. 390) illustrated a series of reefs surrounded by shale and indicated that *Dubaria* occurred in direct association with the reefs. Other illustrations (Termier and Termier 1960, figs. 391 and 394) show *Dubaria* associated with algal limestone from the reefs. Johnson (1975, p. 16) inferred that *Dubaria* from the upper Lochkovian of Bathurst Island was also associated with reefs. Elsewhere the ecological setting of the genus cannot be ascertained from the available data.

COMPARISON OF ECOLOGICAL SETTINGS OF *DUBARIA* AND *ATRYPOIDEA*

Atrypoidea Mitchell and Dun, 1920 which is very common in the Ludlow strata of Arctic Canada, is morphologically similar to *Dubaria*. *Atrypoidea* differs, however, in not having dental lamellae in the pedicle valve. Most *Atrypoidea* appear to have inhabited a soft-substrate in quiet-water, subtidal environment (Jones 1982) and thus occupied a different ecological niche than that proposed for *Dubaria*. However, one species of *Atrypoidea* did develop the ability to inhabit reefs and/or the skeletal sands surrounding the bioherms (Jones and Narbonne 1984). In the areas between the reef only *A. foxi* occurs (Jones 1974). *Atrypoidea biolierma* has an external morphology directly comparable with that of *D. varians*. Both have a similar overall shell form, both apparently had functional pedicles, and both developed rectangular-shaped deflections of the anterior commissure.

TEXT-FIG. 4. Pedicle, lateral and anterior views of *Dubaria varians*, × 1.5, specimens are from sample 256367 (Table 1) and are deposited in the Geologisk Museum, Copenhagen. A–C, MGUH 16097; D–F, MGUH 16098.

CONCLUSIONS

Dubaria and *A. bioherma* sp. nov. both inhabited quiet-water, cryptic habitats associated with reefs. The similarity in the external morphology of the *Dubaria* species and *A. bioherma* strongly suggests that this general morphological scheme was adapted specifically for such a habitat. In particular, the rectangular form of the anterior deflection of the commissure appears to have been a necessity, presumably in some way assisting the feeding process. Comparison with similar modern reef-dwelling brachiopods suggests that predation or more likely competition from other organisms restricted their occurrence to such cryptic habitats. This may explain why *Dubaria* apparently does not occur in quiet-water environments of a more open aspect (for example, in quiet-water lagoonal deposits). The result of such spatial restriction is that brachiopods such as *Dubaria* have a very patchy stratigraphic occurrence.

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